

TWO NEW SPECIES OF HERBACEOUS LYCOPODS FROM THE DEVONIAN OF VENEZUELA WITH COMMENTS ON THEIR TAPHONOMY

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ABSTRACT. Two new species of herbaceous lycopods, *Haskinsia sagittata* and *Colpodexylon cachiriense*, are described from Devonian strata in the Cano Grande–Rio Cachiri region (north central Sierra de Perija) of Venezuela. The recently discovered diverse assemblage of megafossils also contains the first record of progymnosperms in South America as well as possible cladoxylaleans. The lycopods exhibit a number of preservation forms, and these are related to their putative preservational history. The assemblage is of Laurentian aspect, showing greatest similarity to those from New York State. Its biogeographical significance is briefly discussed in relation to the distribution of continents in Devonian times.

MOST of our knowledge of terrestrial vegetation in Devonian times derives from assemblages collected in North America, Europe, and Asia (Chaloner and Sheerin 1979; Banks 1980; Gensel and Andrews 1984). With the exception of Australia, records from southern continents are based on fragmentary, usually poorly preserved megafossils which often lack independent faunal or palynological evidence for their age. In the course of a biostratigraphical study of Devonian outcrops in northern Venezuela, one of us (J. L. B.) and Dr. P. Rachebouef (University of Brest) discovered a completely new fossil plant assemblage, more diverse and better preserved than hitherto recorded from the Devonian of South America.

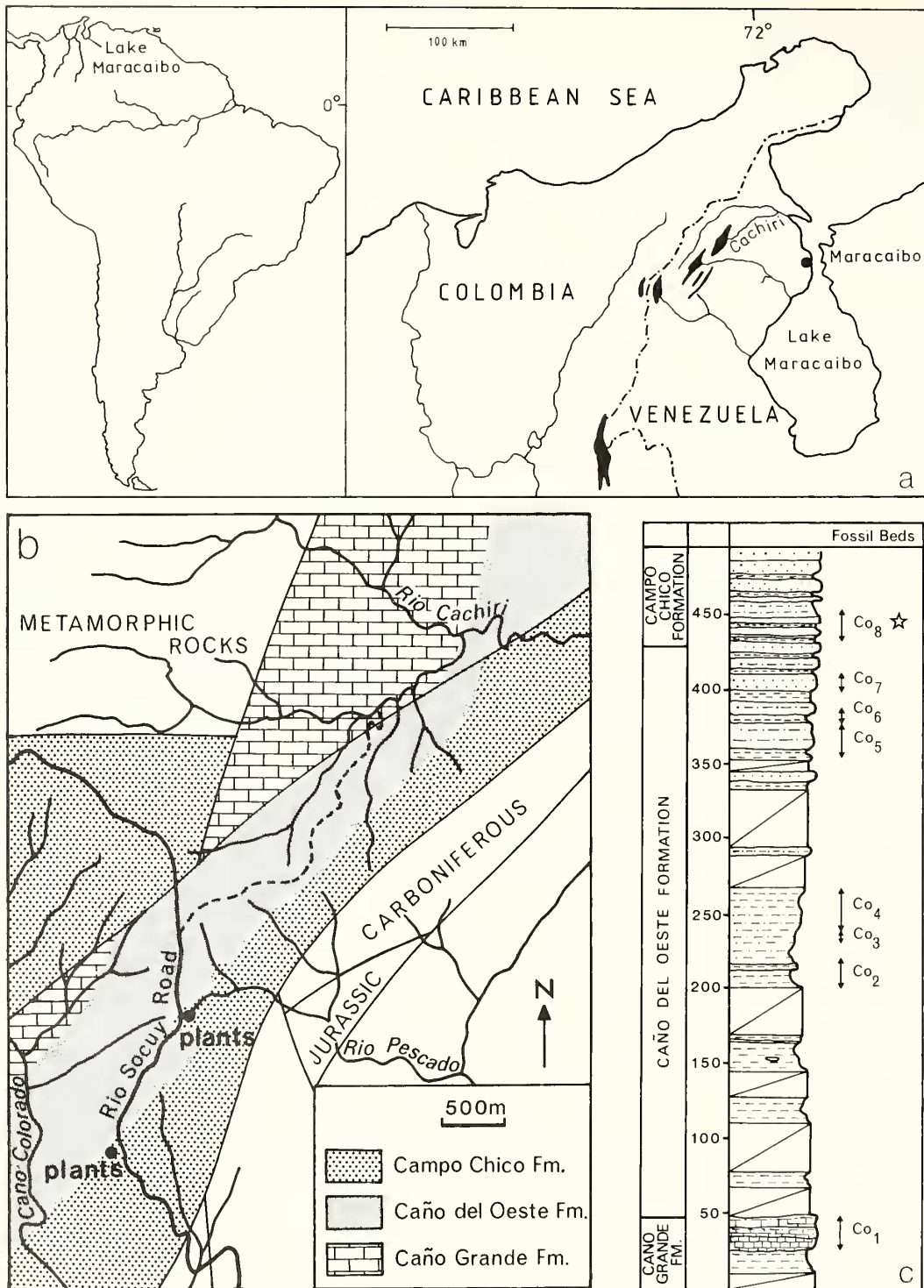
STRATIGRAPHY AND LOCALITIES

The Devonian of the Colombian–Venezuelan basin in the northern Andes comprises a number of outcrops extending from the eastern cordillera in Colombia to the Sierra de Perija in Venezuela (text-fig. 1*a*). The strata exposed in the Cano Colorado–Rio Cachiri area, c. 70 km west of Maracaibo, are the most northerly (text-fig. 1*b*). The geology and biostratigraphy of the area have been summarized by Benedetto (1980, 1984). The fossil plants occur at two exposures of the same horizon (Co₈) towards the base of the Campo Chico formation in the Cano Colorado section (text-fig. 1*c*). There were no animal fossils present, but a rich brachiopod fauna collected about 50 m below the plant beds (Co₆ horizon) is of Givetian age.

MATERIAL AND METHODS

The fossil plants occur in laminated micaceous siltstones ranging in colour from a light olive grey to whitish or pinkish buff depending on the degree of weathering. The lycopod stems are strongly compressed and usually incompletely preserved. Many comprise a thin fragmentary layer of fine-grained sediment sandwiched between two coalified layers. Others are iron-stained impressions often with a dusting of coaly matter. The complete range of preservation forms is discussed more fully below.

All specimens were photographed under uniform and unilateral lighting. The most useful technique for this extremely soft matrix was *dégagement* (Leclercq 1960), tungsten wire sharpened in molten sodium nitrite being used to loosen the grains of sediment. Areas of cuticle were removed on



TEXT-FIG. 1. *a*, locality map indicating Devonian outcrops in the northern part of the Colombian-Venezuelan basin of South America. *b*, Devonian geology in the Cano-Colorado-Rio Cachiri region. *c*, Stratigraphical log of the section along the road to the Rio Socuy from the Cano Colorado. Plant horizon is indicated by a star. Co₁₋₈ refer to horizons with faunal assemblages recorded in detail by Benedetto (1984).

cellulose nitrate film pulls. Latex replicas (Dunlop) taken from impressions with cellular imprints were coated with gold and examined by SEM. Palynological samples were prepared by standard techniques.

The specimens and preparations are housed in the Palaeontology Laboratory, University of Brest, France (prefix LPB).

SYSTEMATIC PALAEONTOLOGY

Class LYCOPSIDA

Order PROTOLEPIDODENDRALES

Family HASKINSIACEAE Grierson and Banks, 1983

Genus HASKINSIA Grierson and Banks, 1983

Type species: *Drepanophycus colophyllus* Grierson and Banks, 1963 (transferred to *H. colophylla* by Grierson and Banks 1983) from the Kiskatom Formation, Tioughniogan Stage, Erian Series, Middle Devonian (= Givetian) in New York State, U.S.A.; also recorded from Lower Frasnian strata of New York State.

Haskinsia sagittata sp. nov.

Plate 71, figs. 1–8; Plate 72, figs. 1–13; Plate 73, figs. 1–8; text-fig. 2

Derivation of name. Latin *sagitta*, arrow, referring to the arrowheaded shape of the leaf.

Holotype. LPB16046 (Pl. 71, fig. 6; Pl. 72, figs. 1, 2, and 12).

Locality. Exposures on the road from the town, Villa del Rosario, to the Socuy River in the Colorado valley, some 950 and 1500 m NNW of the farm 'Alemania', c. 70 km west of Maracaibo, north-western Venezuela.

Horizon. Carbonaceous lutites at base of the Campo Chico Formation; Devonian (?Givetian–Frasnian).

Diagnosis. Herbaceous lycopod with occasional dichotomous branching. Axes at least 10.5 cm long, 4.8–6.8 mm wide ($\bar{x}$ = 5.7 mm, n = 34) exclusive of leaves. Longitudinal lines separate leaf bases. Leaves spirally arranged, sometimes pseudowhorled; 7–9 leaves per gyre (usually 7). Lateral margins of adjacent leaf blades touch or overlap: apices of leaves of one gyre at same level as bases of leaves in that above. Leaves simple and upright, comprising petiole 0.45–1.2 mm wide ($\bar{x}$ = 0.7 mm, n = 35) widening into conspicuous lamina, at maximum width 1.13–1.92 mm ($\bar{x}$ = 1.48 mm, n = 30) with two downwardly directed lateral projections and tapering into an acuminate tip. Leaf length, including petiole, at least 2.47 mm.

Description. Seven small slabs, almost all of slightly differing lithology, contain some forty sterile leafy stems of variable appearance. The variability is due to different forms of preservation and planes of fracture. With one exception (LPB16051, Pl. 71, fig. 2) the possession of distinctive sagittate leaves indicates that the stems belong to a single taxon.

Stem morphology: Except in the two branching specimens the stems show little change in diameter along the short lengths available for study. Branching is dichotomous (Pl. 71, fig. 1). Depending on the preservation/fracture state the stem surface displays elevations or depressions, sometimes both, marking the attachment of leaves, the surface between the leaf bases being smooth (Pl. 71, fig. 2). Leaves borne on the straight margins of the stem are falcate in profile. Further conspicuous features of a few stems are longitudinal dark lines (Pl. 71, fig. 1) which, on any one surface, pass between but not across leaf bases: their number is thus related to the number of orthostichies. They are either parallel or curve slightly outwards around a leaf base. In a few cases much finer, closely spaced, longitudinally orientated striations occur on a thin brown layer, presumed to be cuticular, but when this is removed on a film pull no further detail is visible. A similar patterning is present on a few impressions, but again scanning electron micrographs of latex casts of these stems failed to reveal any precise details of surface cells (Pl. 73, fig. 8).

Leaf morphology and arrangement: Leaves are most commonly seen in profile. A typical example before uncovering (Pl. 72, fig. 5) shows a prominent base tapering upwards into a simple linear blade, which in this case is parallel to the edge of the axis, but may occasionally be directed away from it (Pl. 72, fig. 6). Removal of

sediment between the leaf and axis, and sometimes removal of the axis itself, reveals an approximately parallel-sided petiole and approximately half of a lamina with a downwardly directed lobe (Pl. 72, fig. 8). The tapering apex of the lamina often extends down into the matrix, so that the length of the leaf is actually greater than that visible in profile. At its base the petiole is vertically extended in cross-section, becoming circular and then flattened distally in the same plane as the lamina. The presence of a thick layer of coalified material suggests that the petiole possessed abundant, probably peripheral, strengthening tissues. Except for one fortuitously fractured specimen (Pl. 71, fig. 4) leaf shape in face view was elucidated by *dégagement*. Text-fig. 2, where all the leaves are drawn to the same scale, summarizes the range in shape. The leaf blade is roughly triangular with entire margin, and widest point more or less at the level of the junction of the petiole (Pl. 72, figs. 9–11). Two pronounced downwardly directed projections produce the sagittate form (Pl. 72, figs. 9–11) but very occasionally these flare outwards so that the overall shape is hastate (Pl. 72, fig. 12). A midrib is absent. The parallel-sided petiole widens slightly below the blade, but the actual junction is impossible to define. We are not sure of the exact shape of the extremities of the leaf blades since removal of a few grains of sediment can radically alter a tapering outline. At the leaf apex the blade frequently fades away as if it were thinner distally (Pl. 71, figs. 6 and 8). Evidence from isolated tips and iron-stained impressions in addition to uncovered specimens suggests that the apices were originally acuminate (Pl. 71, fig. 7; Pl. 72, fig. 11). The measurements for leaf lengths (blade plus petiole = 2.47–4.7 mm, $\bar{x}$ = 3.2, n = 19) are therefore too low. The downward projections were probably pointed, but ended somewhat more abruptly than the apices. Any cuticle remaining on blades or petioles is featureless.

The positions of leaf bases on the stems indicate that the leaves were borne in a low spiral, sometimes approaching a pseudowhorled condition, with 7 to 9 leaves in a gyre, the former being the more usual number. The external appearance of leafy shoots in life must have been similar to that of the fossils figured in Plate 71, fig. 4, where the plane of fracture passes through the laminae of the leaves leaving a dusting of coalified material on part and counterpart. The width of this specimen is explained by a change in level which more or less bisects the leafy surface longitudinally and indicates that there were probably two axes lying side by side. The fortuitous and very informative fracture is thus even more remarkable. The subtending stems, originally completely obscured by leaves and sediment, were revealed by *dégagement* on the larger block. Adjacent leaves in a single gyre meet or just overlap at their lateral extremities and the attenuated leaf apex just extends beyond the base of the petiole in the gyre above. From the attitudes of the leaves it seems that the blades were rigid in life but gently curved inwards and tangentially so that they formed a continuous sheath around the stem.

Comparisons. Grierson and Banks (1983) review Palaeozoic herbaceous lycopods, including the families Drepanophycaceae, Protolepidodendraceae, Archaeosigillariaceae, Eleutherophyllaceae, and Lycopodiaceae. The Venezuelan specimens most closely resemble their new taxon, *H. colophylla*. They originally (1963) placed the leafy remains from New York State in *Drepanophycus*, but new information on the leaves, originally considered falcate, and on stem anatomy, led to the generic reassignment. The leaves of the American specimens are not as markedly sagittate and the vertical files of strengthening cells in the outer cortex are more sinuous. On the basis of such differences, and because the Venezuelan plants lack anatomy, we regard them as a new species.

EXPLANATION OF PLATE 71

Figs. 1–8. *Haskinsia sagittata* sp. nov. 1, LBD16050, branching, leafy stem with traces of coalified material, $\times 1.7$. 2, LBD16051, leafless stem, probably attributable to *H. sagittata*, seen at base as a cleavage compression (*sensu* Chaloner and Collinson 1975) and as a cleavage impression distally. Note persistence of coalified material at points of departure of leaves and on truncated petioles attached to sides of stem, unilateral illumination, $\times 2.8$. 3–5, LBD16052. 3, coalified stem with sedimentary infill (s) and one uncovered leaf (arrowed), $\times 2.8$. 4, leaf lamina cleaved compressions of two aligned stems, $\times 3.7$. 5, base of stem illustrated in fig. 3, unilateral illumination, $\times 10$. 6, LBD16046, uncovered leaf on holotype. It was attached ('scar' is arrowed) to lower surface of the stem and shows the typical lateral displacement of the petiole, $\times 11$. 7, LBD16054(i), acuminate apex of leaf, probably incomplete at tip. Note that it ends at approximately same level as base of leaf above. 8, LBD16046, petioles and lamina bases of three leaves uncovered above fractured end of ridged stem. Arrowed is the elongate raised area in the oval depression marking attachment of petiole on lower surface, $\times 10$. (Photographs under uniform illumination except where otherwise stated.)



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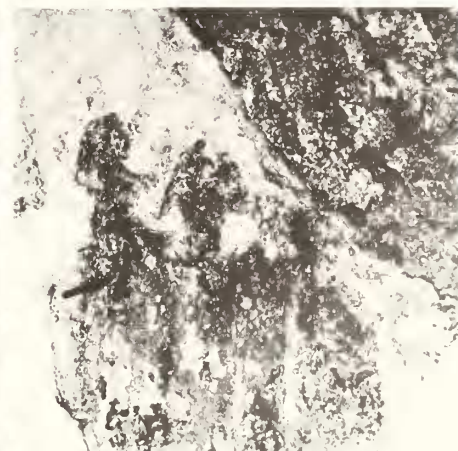
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There remain a number of very fragmentary fossils with similarly shaped leaves, which on further investigation may be assigned to *Haskinsia*. Grindley *et al.* (1980) described some stems from the Middle Devonian of Marie Byrd Land, western Antarctica, with similar dimensions and numbers of leaves per gyre. The leaves themselves are slightly smaller but rarely completely preserved, and are sickle-shaped in profile. Face view drawings of the leaves show that their shape is variable: the one just below no. 3 in their fig. 10 has a downwardly projecting tip on the left hand side reminiscent of *H. sagittata*. A major difference is the presence of a central line presumably representing a vein or midrib in the Antarctic specimens. The latter were placed in a new species, *D. schopfi*, but on the basis of leaf shape they clearly do not belong to that genus (Grierson and Banks 1983).

Far more problematic are the short lengths of lycopod stems, usually lacking leaves but with leaf bases or scars, that are superficially similar to some of the preservation forms seen in the Venezuelan material. These include *Haplostigma furquei* from the Middle Devonian of Argentina (Frenguelli 1954), *H. irregularis*, Middle Devonian of Brazil (Kräusel 1960) and the Falkland Islands (Seward and Walton 1923) as well as from the type area in South Africa, and *Palaeostigma sewardi* first described from the Middle Devonian of Brazil (Kräusel and Dolianiti 1957). The most recent assessment of these two genera is in a preliminary survey of South African Palaeozoic floras by Anderson and Anderson (in press). They note that *Palaeostigma* is atypical among South African lycopods in that it invariably occurs as impressions with the leaves or granulae of the lower surface of the stem showing through to the upper. We have described this preservation state in *Haskinsia sagittata*, but the taxa differ in that the Andersons interpret the projections and depressions on the stem as leaves, describing them as 'rudimentary, rounded to oval granulate projections about as high as wide, well spaced, irregularly aligned into imperfect low angle spiral'. *Haplostigma*, originally based on South African material, has a more regular appearance and the leaves although rarely preserved are described as 'squat conical, acute tipped, length around 1 to 2 times basal width with gentle distal inclination'. Anderson and Anderson placed *H. furquei* in synonymy with *H. irregularis*. We have not had the opportunity to examine specimens of either genus, but from photographs it seems that their relatively featureless stems more closely resemble leafless *Haskinsia sagittata* than those lycopods with a characteristic surface patterning such as *Archaeosigillaria*. The latter, represented by *A. picosensis* (placed in synonymy with *A. caespitosa* by Anderson and Anderson (in press)) occurs with *Protolpidodendron kegei* at the same Middle Devonian horizon as *Palaeostigma sewardi* in Brazil. It is easily separated from *H. sagittata* (as is *A. conferta* from Argentina (Menendez 1965a)) on the grounds of leaf base characteristics (Kräusel and Dolianiti 1957).

Finally a predominantly lycopod flora from the late Silurian–early Devonian of Libya (Klitzsch *et al.* 1973; Boucot and Gray 1982) contains a number of fragmentary stems with leaf attachment sites, but not leaves, visible. Their preservation states appear to parallel some of those we have described. In particular, the illustrations of *Protolpidodendron helleri* (Klitzsch *et al.* 1973, figs. 1, 12, 13) and *Precyclostigma tadrartense* (ibid., figs. 2, 6, 9, 10) resemble *H. sagittata* in size, leaf arrangement, and

EXPLANATION OF PLATE 72

Figs. 1–13. *Haskinsia sagittata* sp. nov. 1, 2, LBD16046, holotype. 1, stem with some uncovered leaves. Those near the base are attached to the upper surface of the stem, $\times 2.4$. 2, unilateral lighting to show surface features such as leaf bases and ridges, $\times 2.6$. 3, 4, LBD16047, pink stem impressions with dusting of coaly powder. 3, $\times 1.4$. 4, unilateral illumination, $\times 1.7$. 5–7, leaves in profile before uncovering. 5, LBD16052, $\times 9.4$. 6, LBD16047, $\times 10$. 7, LBD16049, $\times 7$. 8, LBD16047, half of leaf revealed on removal of overlying stem and matrix, $\times 9$. 9–11, face views of uncovered leaves. 9, LBD16047; 10, 11, LBD16052 all $\times 10$. 12, LBD16046, hastate leaf exposed when sediment was removed from above holotype; probably attached to upper surface of stem, $\times 12$. 13, LBD16052, stem on left has more or less continuous covering of coalified material (leaf attachment sites are more obvious under unilateral illumination) and shows numerous leaves in profile, successive gyres being close together, $\times 1.6$. (Photographs under uniform illumination except where otherwise stated.)



EDWARDS and BENEDETTO, *Haskinsia sagittata*

the presence of longitudinal grooves between leaf bases, although there are differences in the orientation of the leaf bases. In contrast the much larger leafy lycopod axes recorded from the overlying Lower Devonian Tadrart Formation (Lejal-Nicol 1975) are completely different and more comparable to arborescent forms reported from later in the Devonian elsewhere (Chaloner and Sheerin 1979).

Order PROTOLEPIDODENDRALES
Family PROTOLEPIDODENDRACEAE Kräusel and Weyland, 1949
Genus COLPODEXYLON Banks, 1944

Type species. *Colpodexylon deatsii* Banks, 1944 from the Delaware River Flags, equivalent to the marine Upper Ithaca or Enfield formation, Finger Lakes Stage, Senecan Series, lower Upper Devonian (= Frasnian) of New York State, U.S.A.

Colpodexylon cachiriense sp. nov.

Plate 73, fig. 9; Plate 74, figs. 1–9

Derivation of name. From the Rio Cachiri, after which the most northern outcrop of Devonian rocks in Venezuela is named.

Holotype. LPB16045 (Pl. 74, figs. 1 and 2).

Locality. Roadside exposures on the road from the town, Villa del Rosario, to the Socuy River in the Colorado valley, some 950 to 1500 m NNW of the farm 'Alemania', c. 70 km west of Maracaibo, north-western Venezuela.

Horizon. Carbonaceous lutites at the base of the Campo Chico Formation, Devonian (?Givetian–Fresnian).

Diagnosis. Vegetative stems at least 10 cm long, 5.3 to 9.5 mm wide ($\bar{x}$ = 7.7 mm, n = 10) with persistent leaves borne spirally or in pseudowhorls. Leaf bases not contiguous with 7–9 leaves per gyre (9 being the commonest number); successive gyres also widely spaced. Stem surface between leaf bases probably smooth. Divaricate leaves with broad, flat, or abaxially curved bases, three forked; 0.62–0.96 mm ($\bar{x}$ = 0.76 mm, n = 14) wide in basal unbranched region, trifurcating 4.0 to 7.5 mm ($\bar{x}$ = 5.6 mm, n = 11) from attachment. The central fork (0.5–0.72 mm) is approximately twice as wide as the laterals (0.26–0.3 mm) and at least twice as long. All tips acuminate. Leaves at least 14.7 mm long.

EXPLANATION OF PLATE 73

Figs. 1–8. *Haskinsia sagittata* sp. nov. 1, LBD16050, short length of stem with coalified covering, prominent ridges, and leaf bases with sedimentary infill (text-fig. 3*d, e*), $\times 3$. 2–6, LBD16046. 2, part of lower surface of rock bearing holotype showing predominantly impression fossils, unilateral illumination. Lustre surface produces brighter areas. Note range in form of projection marking bases of leaves attached to upper surface, $\times 2.4$. 3, area of left-hand stem in fig. 2 magnified to show detail of such projections and the infilled bases of leaves (arrowed) attached on lower surface of stem, $\times 6$. 4, two stems on same surface as holotype; latex cast made from one on right, unilateral illumination, $\times 3.1$. 5, part of stem on same surface as holotype, lighter areas comprise fine-grained sedimentary infill; darker areas comprise granular coalified material. Inverted Us mark sites of attachment of leaves on lower surface, $\times 9.2$. 6, oval area marking attachment of leaf passing down into matrix; powdery coalified material has been removed to reveal sediment filling base of petiole, $\times 20$. 7, scanning electron micrograph of indeterminate spores recovered on surface of latex cast (stub no. 620), $\times 650$. 8, scanning electron micrograph of latex cast of stem impression illustrated in fig. 4 (stub no. 628), $\times 16$.

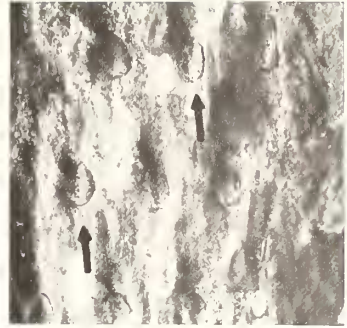
Fig. 9. *Colpodexylon cachiriense* sp. nov. LBD16052(i), coalified compression fossil with very fine-grained sedimentary infill (s) sometimes iron-stained on surface (r) and near base an uncovered trifurcating leaf extending from a crescentic depression on lower surface. Arrow indicates possible vascular strand, $\times 29$. (Photographs under uniform illumination except where otherwise stated.)



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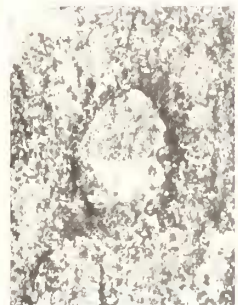
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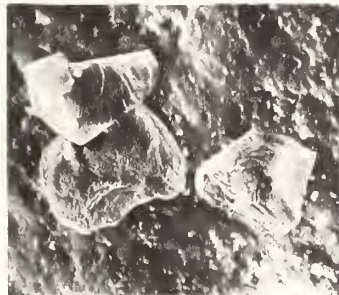
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Description. The diagnosis is based on short lengths of unbranched stems showing a variety of preservation forms united in the possession of trifurcating leaves. Apart from two isolated impressions, all the leaves were uncovered. As they are small in number and generally incomplete or distorted, we anticipate that the dimensions recorded in the diagnosis will be emended on the discovery of further specimens.

Stem characteristics: The parallel-sided stems are almost featureless except for the presence of leaf bases or attachment sites marked by inverted crescentic (Pl. 74, fig. 7) or more strongly arched lines (Pl. 74, fig. 1) enclosing depressions and, less frequently, by inverted crescentic ridges. The persistent leaves vary in their arrangement from pseudowhorled to a more steeply pitched spiral condition, but in all cases successive gyres are widely spaced, as are individual leaves in a gyre. The number of leaves per gyre ranges from 7 in the narrower stems to 9 or possibly more in the wider, uncertainty arising from the fact that usually only one surface of a stem is preserved.

Some evidence of a vascular strand comes from a stem 9.5 mm wide, with a longitudinal strip of sedimentary infill and coalified material 1 mm wide, bearing coarse longitudinal striations (arrowed in Pl. 73, fig. 9). The coalified material was macerated in Schulze's solution, but no tracheids were recovered. Latex replicas taken from rock surfaces show faint impressions of cells, but failed to reveal further detail under the SEM.

Leaf characteristics: The most complete leaves are long, slender, and trifurcating, showing no distinction between petiole and blade. (Pl. 74, figs. 2, 4, 5). The proximal unbranched region is parallel-sided and strongly flattened in the plane of the trifurcation, widening slightly before branching. The crescentic attachment sites and bases of leaves uncovered below such sites (Pl. 74, fig. 8) suggest that the basal region was abaxially curved, but this is not apparent on the leaves attached to stems fortuitously fractured transversely (Pl. 74, fig. 7). Nor do they show the broad longitudinal grooves visible on the proximal regions of some of the more complete leaves (Pl. 74, figs. 2 and 3).

Almost all the branching leaves were uncovered. The lateral segments are usually slightly more than half the width of the central one, the three separated basally by U-shaped embayments of sediment where all are preserved in the same plane. All three taper, the lateral ones being much shorter than the central. We doubt that any of the extreme tips remained intact after uncovering as the sediment grains were wider than the distal parts of the leaves, which were very easily dislodged. Vague outlines of cells are visible as impressions of the adaxial surface near the base, but no further anatomical details of the leaf were obtained. The leaves were persistent, but in the majority of cases only the divaricate basal parts are preserved showing tapering (Pl. 74, fig. 7), truncated (Pl. 74, fig. 9), or more rarely, hooked tips (Pl. 74, fig. 3). Such incompleteness suggests that the branches were more delicate and also explains the change in orientation sometimes observed between the two regions. Whether or not the entire leaf in life was a stiff spreading organ with all parts in the same plane, or was more flexuous, as seen on the holotype, remains conjectural.

All the leaves were sterile. However, we noted two isolated possible sporangia preserved near typical axes. One is elliptical and featureless; the other, 2.5 mm long and 1.8 mm wide, has a notch at one end which is extended into a central longitudinal depression (Pl. 74, fig. 6). Neither structure yielded spores and we have no evidence, apart from association, that they belonged to *C. cachiriense*.

Comparisons. The diagnosis of *Colpodexylon* is based on sterile and fertile leafy stems from the Devonian of New York State (Banks 1944). Most are compression fossils, but some have pyritized

EXPLANATION TO PLATE 74

Figs. 1-9. *Colpodexylon cachiriense* sp. nov. 1, LBD16045, holotype, impression fossil, unilateral light showing attachment sites of leaves borne on the lower surface of the stem, $\times 1.8$. 2, enlargement of part of holotype to show the single attached trifurcating leaf, $\times 3.6$. 3, LBD16048, impression fossil with incomplete attached leaves with hooked tips, unilateral illumination, $\times 3.3$. 4, LBD16049, iron-stained impression of leaf with traces of coalified material, central segment of trifurcation missing, $\times 4$. 5-8, LBD160148. 5, detached leaf with incomplete tips, $\times 3.7$. 6, possible isolated sporangium, $\times 10$. 7, coalified stem with leaf bases in profile. Arrow indicates another stem fractured transversely showing abaxial or adaxial surfaces of leaf bases, $\times 2$. 8, distal part of stem figured in fig. 7, preserved as impression fossil. Leaf scars have been developed to expose adaxial surfaces of two leaves (arrowed) originally projecting down into the matrix below the stem. Isolated leaf shows two of the three distal segments and typical curvature just below the trifurcation, $\times 7.4$. 9, LBD16045, stem impression on same surface as holotype. Incomplete leaves show fracture at point of attachment (arrowed), $\times 5$. (Photographs under uniform illumination except where otherwise stated.)



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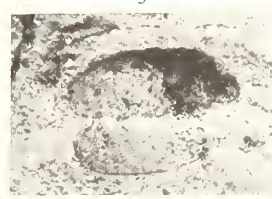
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anatomy. The Venezuelan plants, although far more fragmentary and lacking both reproductive and anatomical details, are assignable to *Colpodexylon* because they possess persistent trifurcating leaves which Grierson and Banks (1963) considered 'the chief diagnostic character' (p. 253) of the genus. Banks originally distinguished two species, the type *C. deatsii* from Frasnian strata and the anatomically less completely known *C. trifurcatum* from the Eifelian. The two are readily separated from the South American plant in that their stems bear a greater number of leaves per gyre with leaf bases both laterally and vertically contiguous. The preservation of the Venezuelan plants is such that usually only the inside of leaf bases are visible, but these are so widely spaced that considerable areas of stem surface must have been exposed between leaf bases. There are however certain similarities in the structure of the leaves. When describing the basal segment of the leaf of *C. deatsii*, Banks (1944) noted that it was necessary to remove matrix from 'alongside the leaf margin in order to expose the true widths' (p. 654) and concluded that this was evidence for a slightly revolute margin. He also recorded two longitudinal furrows on the leaf surface. In describing isolated sporangia he mentioned that a few showed an apical notch sometimes extended into a median line. These were not illustrated but may be similar to the isolated structure we figure in Plate 74, fig. 6.

Lemoigne and Ishchenko (1980) described a putative third species from the Famennian of the Ukraine. In the leaves, only the lateral branches beyond the trifurcation are visible (a similar preservation to that illustrated in Pl. 74, fig. 4), the authors suggesting that the central one is present in a different plane. The stem surface looks quite different from the other species including *C. cachiriense* because each leaf base has an adaxial depression. The leaves are considered ligulate.

Of the herbaceous lycopods reported from South America the only taxon with distinctly divided leaves is *Protolpidodendron kegelii* (Kräusel and Dolianiti 1957) from the Maranhao Basin of Brazil. The leaves as illustrated differ from those in *C. cachiriense* in that they resemble tuning forks, being at least 15 mm long with a bifurcation about 2 mm from the base, although there is always the possibility that further uncovering will show them to be more complexly branched.

TAPHONOMY

Several recent investigations demonstrate that both the type of preservation and subsequent planes of fracture are responsible for the diversity of appearance in the stems of herbaceous and arborescent lycopods (Chaloner and Collinson 1975; Thomas and Purdy 1982; Grierson and Banks 1983; Rex and Chaloner 1983). Such studies greatly facilitate interpretations and descriptions of our fossils and, in particular, the leaf bases of *H. sagittata*. Indeed, the leafy specimen illustrated in Plate 71, fig. 4 allows a leaf lamina cleaved compression plane to be added to the fracture plane terminology summarized by Grierson and Banks (1983). However it has sometimes been difficult to apply their terminology, based mainly on coalified compression fossils, to the heavily weathered Venezuelan examples, where at best the original stem is replaced by a thin layer of sedimentary infill coated by a film of coalified material, and where counterparts are missing. Our fossils exhibit a range of appearances and preservation states (compare, for example, Pl. 71, figs. 1–5) and the entombing sediments vary in colour and hardness, a reflection of the degree of weathering. Some of the more perplexing structures occur in those fossils where little or no organic material remains. The range of types of preservation present permits the poorly preserved forms to be interpreted by reference to the more complete and well-preserved stems. Such an assessment of different preservation types is necessary as the identification and description of lycopods from the Devonian of South America, South Africa, and Antarctica have been based on similar fragmentary impression fossils.

Types of preservation

a. Fossils with layer of sediment sandwiched between two coalified layers that presumably represent the outer tissues of the stem. The amounts of coalified material, sedimentary infill, and compression vary between specimens.

H. sagittata. The least compressed specimen (Pl. 71, fig. 2) lacks the diagnostic leaf blades, but the shape, orientation, and arrangement (7 per gyre) of leaf bases and its size permit assignment to *H. sagittata*. The

coalified stem, a cleavage compression *sensu* Chaloner and Collinson, exposed by a fracture plane running between the upper surface and the matrix is present only at the base of the specimen. A fractured example of the poorly defined elongate projections, the bases of the petioles, show them to be filled with sediment. Leaf arrangement is much clearer where the fossil has dropped out revealing an impression of its lower surface, a cleavage impression. Fine striations are visible under a dissecting microscope.

The stem illustrated in Plate 71, figs. 3 and 5 is similar in composition, but looks quite different as a result of greater compression and irregular fracture removing parts of the upper surface. It comprises a papery layer of very fine-grained whitish sediment(s), stained orange on the outside, and sandwiched between two sporadic powdery coaly layers. Both impression and infill have areas of indistinct cell outlines. Removal of the rock distal to a depression reveals the characteristically shaped leaf of *H. sagittata* (arrowed in Pl. 71, fig. 3). In some cases the depressions are filled with sediment and some additional coalified material producing mounds with irregular topography, but in addition to these, smooth mounds of relatively low relief may be seen on the lower impression surface as well as less regular ones on the sedimentary infill (see Pl. 71, fig. 4 where the stem is illuminated unilaterally). The latter are the incomplete leaf base infills of the leaves attached to the upper surface (i.e. that closer to the observer) and the former show that the stem has been so compressed that its lower surface is pressed into the bases of these leaves producing these 'false leaf bases' (text-fig. 4e, f). Their positions indicate that they do not represent the inward collapse of the stem between leaf bases on the lower surface.

C. cachiense. The most complete fossils are of this preservation form. The unbranched stem (40 mm long) in Pl. 73, fig. 9, has a variable appearance due to uneven fracture. The extremely fine-grained infill is silvery internally (s) but iron-stained on the surface (r). It lies above a thick coalified layer, but a similar layer representing the organic remains of the stem closer to the observer is rarely preserved above the sedimentary infill. The impression fossil on the rock below is also iron-stained and while some areas bear faint traces of cells, others are distinctly warty. The sediment infill does not extend to the edges of the stem which are marked by a strip of coaly material of variable width (0.3–0.4 mm) although this has sometimes broken. The bases of leaves attached to the sides of the stem, represented by tapering, needle-like projections before developing, are heavily coalified compressions continuous with this marginal band. The attachment sites of the widely spaced superficial leaves are not conspicuous. On the lower impression surface they are shallow depressions limited at one end by a crescentic coalified line. The depression is sometimes filled with sediment and additional coalified material. On the cleaved sedimentary layer their positions are marked by short transverse furrows. Attachment sites on the upper surface of the infill are marked by crescentic ridges, abruptly truncated on the convex edge and tapering gradually on the other. They are most conspicuous where the surface stain has rubbed off.

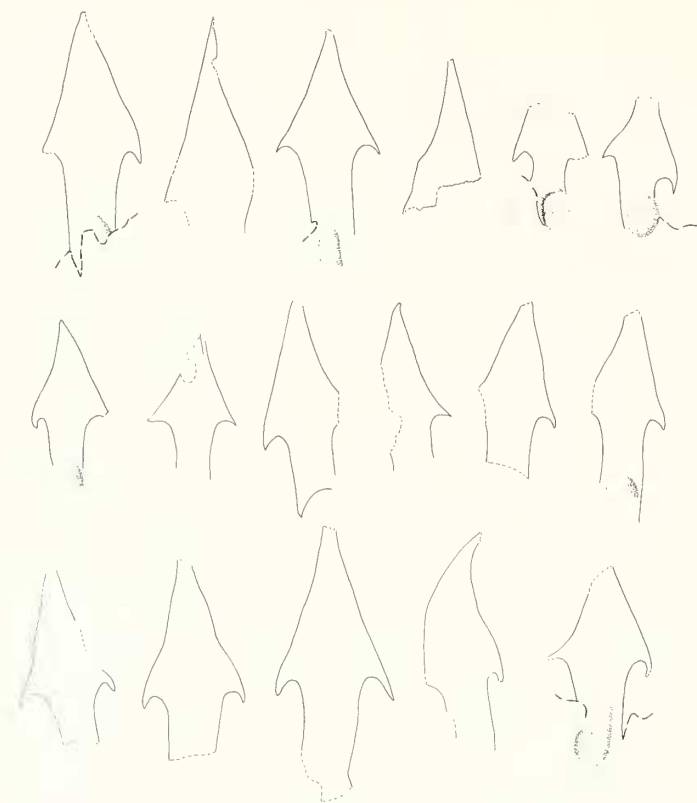
Another example (Pl. 74, fig. 7) has a more untidy appearance because the layers of coalified material and sediment are not continuous over wide areas. They are easily dislodged; the impression below has been developed (Pl. 74, fig. 8) to demonstrate the broad abaxial curved junctions between leaves and stem.

b. Strongly compressed fossils comprising a granular mixture of inorganic and coalified material, only rarely showing distinct layering.

H. sagittata. The holotype and about twenty other axes occurring at different levels in the rock, but most orientated in the same direction, show this preservation type. The matrix was the least weathered of all the slabs examined. The specimen provided an opportunity to study part and counterpart as during preparation one stem was split. Its plane of fracture was irregular but more fossil remained on one surface (the part) than the other (counterpart) thus paralleling the situation on the two major faces of the rock. The surface equivalent to the part bears a number of stems of variable colour (ranging from grey to brown to rust) and appearance. Depending on the plane of fracture and amount of weathering or damage since collection, granular sediment, sporadic coaly or rusty material or stained rock below may be exposed. In some areas the impression beneath has a metallic sheen, the entombing sediment being much finer grained than the general matrix and displaying longitudinally aligned evenly spaced depressions presumably representing the outlines of epidermal cells. SEM examination of latex casts of such stems failed to show the precise shape of individual cells (Pl. 73, fig. 8). The predominantly impressions on the reverse of the block (equivalent to the counterpart) are similar in appearance ranging from those with a striking gold-lustre surface (Pl. 73, fig. 2) to those stained brown and visible only in unilateral lighting.

Before developing only a few leaves were visible in profile, but removal of sediment above and adjacent to stems showed that they were ensheathed in leaves, slightly smaller than the mean, but identical in shape (see base of holotype; Pl. 72, figs. 1, 2 and Pl. 71, fig. 8).

The most conspicuous macroscopic features of these axes, enhanced by unilateral illumination, are the depressions and elevations, the latter sometimes standing over a millimetre above the stem surface marking the positions of leaves. Here again the positions of the bases of leaves of both sides of the stem may be visible on one



TEXT-FIG. 2. Outlines of uncovered leaves showing range in shape and size, drawn from specimens LPB16046, 16047, 16049, 16052, and 16054. All $\times 24$.

exposed surface. The depressions marking the leaves passing down into the matrix are most clearly defined and, on the parts, have three different appearances. In the complete absence of the compression fossil they appear as inverted Us (Pl. 73, fig. 5), often delimited by a line of coalified material (the remains of the peripheral tissues of the leaf base), enclosing a shallow depressed area which sometimes bears a central, longitudinally aligned fold (Pl. 71, fig. 8; text-fig. 2). More usually the attachment site is marked by a circular, elliptical, or ovate area of fine-grained sediment frequently covered by a thin film of coalified matter (Pl. 73, figs. 3, 4, 6). Although this may represent the peripheral tissues of the side of the stem closer to the observer, in a few rare cases, it is further obscured by the infill layer. The plug of sediment may be flat and almost flush with the stem surface or possess a central, barely visible, fold. Finally, less regular mounds of coarser sediment mark the leaf bases.

The elevations are more variable and may be truncated with unevenly contoured tips or more usually are smooth attenuated mounds (Pl. 73, fig. 4). Little sediment or coalified material persists on the flanks of the projections, but occurs sporadically on the surface of the stem particularly in the vicinity of the margins.

The projections are far more distinct on the counterparts accentuated to some extent by the lack of compression fossil. The tips of the pegs are either rounded, irregularly fractured, or have a central crater-like depression surrounded by a rim (Pl. 73, figs. 2 and 3). Depressions or circular to elliptical areas of sediment (sometimes covered by a thin dark layer) mark the attachment of leaves beneath the stem. These may alternate regularly with the pegs or almost coincide with them (Pl. 73, fig. 3).

A few of the stems (e.g. the holotype) bear prominent elongate ridges or depressions of varying lengths (Pl. 72, fig. 2; Pl. 73, figs. 1 and 4). On the specimens equivalent to parts, longitudinally aligned ridges occur between, but never traverse, the leaf base depressions and are sometimes interrupted by the mounds. Between the vertically superimposed depressions they are parallel, 0.6 to 0.9 mm apart, but may widen slightly to enclose the

depressions. Where the body fossil is missing on this surface, ridges also occur on the impression below. A latex replica of such a surface, a cast of the stem (Pl. 73, fig. 8), suggests that the leaves of a single orthostichy were borne on a broad probably slightly raised band isolated from each adjacent one by a groove. On the stems (= counterparts) exposed on the reverse of the slab, longitudinally orientated grooves pass between the projections and across some of the depressions, but there are no ridges.

c. Coalified compressions

One short length of *H. sagittata* stem (Pl. 73, fig. 1) comprises an almost continuous thin layer of coaly material interrupted by approximately circular areas of sediments, thought to be trapped within the bases of leaves attached to the lower surface. Also present are longitudinal ridges separating the leaf bases, and occasional indistinct mounds on the surface of the coalified layer. The latter may mark the portions of the leaves attached to the upper surface of the stem, i.e. that closer to the observer. A very thin film of coaly material has been noted on two of the circular areas of sediment. This may represent the remains of the tissues of the upper surface of the stem. A drawing of a transverse section through this stem is given in text-fig. 3*d*. Unfortunately its counterpart is missing and no further information was gained on removing the sediment overlying one end.

In most fossils of this type the coalified layer is more powdery and rarely continuous, frequently revealing an iron-stained impression on the rock beneath. Such a stem, figured on the left in Plate 72, fig. 13, is typical in that the attachment sites of the leaves on the lower surface are marked by shallow depressions and on the upper by elongate smooth mounds. Leaf bases in a single orthostichy are widely spaced. The stem surface bears numerous faint longitudinal ridges and grooves that are not continuous over any great distance. The stem on the right looks quite different: it has more pronounced relief and less coaly material. The leaves in profile are more numerous. Although approximately the same width, it has at least nine leaves per gyre and successive gyres are more closely spaced.

The most striking fossils in the assemblage are those where the coalified material is replaced by a granular reddish brown layer.

d. Impressions. Many of the fossils available for study were of this type. Some may have been produced by tropical weathering of originally rather fragmentary coalified compressions or coalified material plus sedimentary infill, but others may be artifacts of collecting in that only the counterpart was originally retained and the body fossil may have been dislodged and lost on subsequent transport.

H. sagittata: The weathered specimens obviously intergrade with some of the coalified compressions just described (Pl. 72, fig. 13). All occur in a very soft, buff to pink matrix, one most useful in deducing leaf morphology by uncovering. The stems illustrated in Plate 72, figs. 3 and 4 are pink iron-stained impressions with traces of black powder associated with leaf bases. Also present on parts of the stem and certain leaves is a brown film which may represent the remains of a cuticle, but this lacks cellular imprints.

The leafy stem figured in Plate 71, fig. 1 superficially resembles the cleavage compression illustrated by Grierson and Banks (1983, fig. 4). The most obvious common features are the circular and oval areas of sediment (0.96 mm long and 0.83 mm wide) marking the attachment sites of leaves. In the Venezuelan fossils, just above and slightly to one side of each leaf base is a slight mound, a false leaf base, marking the position of the leaf on the surface nearer the observer. The stems have a high relief but very little organic material persists. Some of this is in the form of a thin layer of cuticle with traces of cellular markings and more prominent widely spaced longitudinally orientated dark lines delimiting orthostichies. These are sometimes replaced by less regular ridges or furrows. Film pulls showed no further cellular detail.

C. cachiriense: The holotype (Pl. 74, figs. 1 and 2) is predominantly an impression fossil, stained dull red towards one end; leaves are preserved as compressions. Their attachment sites are marked by shallow inverted U-shaped depressions containing oval or elliptical mounds of fine-grained sediment plus some coalified material. The curves of the U extend as shallow ridges, almost to the level of the gyre below, giving the striated appearance best seen in unilateral light. The strongly curved junction between leaf base and stem is represented by a pronounced strip of coalified material much greater in thickness than the coalified film, presumed to be the remains of the outer tissues of the stem, exposed on removing the sedimentary infill. Some very low mounds perhaps marking the sites of leaves on the upper surface are just visible between the depressions on the surface of the impression towards its base, but are sometimes superimposed on the sedimentary infill distally.

A representative of the commonest preservation type of *C. cachiriense* is shown in Plate 74, fig. 3. Its surface has a yellow, silky, almost bone-like, texture. Excavations around the ends of similar small fragments indicate that originally present was a crumbling mixture of small irregular sheets of coalified material and sedimentary infill. Leaf attachment sites on the impression resemble those on the holotype, but when sediment and coalified material are removed, the surface of the stem impression is also convex, suggesting that the stem had collapsed

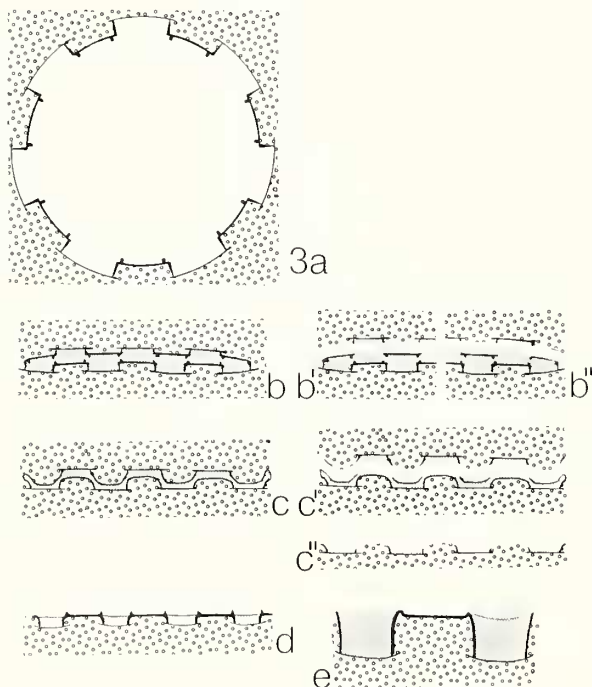
inwards just below a leaf. That this was a topographic feature of the stem in life is considered unlikely: similar but more pronounced examples are seen on stems showing distortion from twisting and stretching.

Preservational history. The sequence of events that produced these preservation forms is broadly similar for the stems of both species. Biodegradation of internal tissues of stems and leaves would have resulted in collapse of these organs, but as emphasized by Rex and Chaloner (1983) exactly when this occurred in relation to burial, possible infiltration by sediment and then further compaction under a mass of sediment, is difficult to determine. The situation is further complicated by the differing rates of decay of soft and hard (strengthening) tissues. Here major problems in interpretation relate to the resilient leaf bases and other strengthening tissues in *Haskinsia* and to the compression of the flat divaricate leaves of *Colpodexylon*.

Impressions of epidermal cells in the extremely fine-grained matrix immediately around some of the fossils suggest that an iron-rich layer quickly encrusted the plant surface after immersion (Spicer 1977). Decay of soft tissues continued during immersion and subsequent burial, but as the stems began to collapse the bases of leaves retained their shape because of the presence of decay-delaying peripheral strengthening tissues. In some instances sediment began to accumulate within the increasingly hollow stems and may well have become trapped in the leaf bases early on, thus further reinforcing them (text-fig. 3). As overlying sediment increasingly compressed the stems perhaps squeezing more grains into the leaf bases, a cast of the inside of the stem surrounded by a very thin layer of disintegrating tissues would have resulted.

Further compression of the infill would have resulted in considerable distortion (Rex and Chaloner 1983) with parts of stem and entombing matrix pressed into leaf bases (text-fig. 3c) thus producing the false leaf bases already noted (Pl. 71, fig. 5). A similarly undulating cross-section would be seen in fossils lacking any sedimentary infill (e.g. Pl. 72, figs. 3, 4, 13). As is often the case features of one surface appear less compressed than the other (text-fig. 3).

Rex and Chaloner (1983) investigating the behaviour of spines in a plant like *Sawdonia* during compression used a hollow cylindrical foam rubber model, which in section looks remarkably like



TEXT-FIG. 3 *a-c*. Diagrams showing postulated behaviour of stem of *H. sagittata* on compression and subsequent fracture. Coarse stippling represents matrix, fine stippling sedimentary infill. For ease of drawing a whorled arrangement of leaves is shown with those at the margin both directed downwards (*a*). The fossil above the fracture is equivalent to the counterpart, that below, the part. *b*, fossil with well-defined coalified layers and sedimentary infill with fracture plane passing between matrix and upper surface of stem and across (*b'*) or around sediment infill of leaf bases (*b''*). *c*, highly compressed fossil with fracture plane passing over upper surface and across leaf bases (*c'*). *c''* shows a weathered example with surface of matrix below the compression exposed. In even more compressed forms, sometimes lacking infill, fracture is less regular across stem surface. *d, e*, postulated section through the stem illustrated in Plate 73, fig. 1 where fracture occurs across upper surface of coalified compression and across bases of leaves attached to lower surface. *e* is enlarged to show detail of the longitudinal ridges.

our stems. On compression the 'spines' on the upper surface became much shorter, those on the lower surface shortened but less so. Thus the rock surface with stems showing the most pronounced depressions and the most compression material (the parts) was probably the original surface of the sediment.

The longitudinal ridges and grooves on some of the preservation forms are more difficult to interpret. The presence of dark lines in similar positions on certain stems (Pl. 71, fig. 1) suggest that they were indeed regions of thick-walled strengthening tissues equivalent to those described for *H. colophylla* by Grierson and Banks (1983) who considered them hypodermal. In many of the Venezuelan examples (type *b*, Pl. 71, fig. 8, Pl. 72, fig. 2; type *c*, Pl. 73, fig. 1) they seem to be part of the stem surface, where they are associated with the leaf bases on the lower surface of the stem. They thus appear as ridges on the impression fossil below that surface, ridges on the body fossil (part), and grooves on the impression counterpart. The latex cast of the lower surface of such a stem (Pl. 73, fig. 8) shows narrow grooves separating broad ridges on which the vertical files of leaves are borne.

The sequence of events that produced such an arrangement remains problematic. Inwardly projecting rods of more persistent hypodermal tissues could have produced longitudinal grooves on the surface of the sediment filling the hollow (decomposed) centre of the stem in a sequence analogous to the production of grooves on pith casts of *Calamites* (text-fig. 3*b*). During further diagenesis the organic matter may have almost disappeared so that the entombing matrix was pressed against the surface of the cast. The resulting impression in the surrounding rock would have longitudinal ridges but these have nothing to do with the original surface of the plant (also seen in *Calamites*). However, in these Venezuelan examples, as there is little or no sedimentary infill, it seems likely that the longitudinal strands themselves projected into the matrix and subsequently became coalified. While preferential preservation may account for their presence on one side only of the stem, it is also possible that the positions of the strands on the two surfaces were coincident on compression, thus reinforcing each other to produce the observed feature. Indeed on stems which are twisted or where leaf bases on the two surfaces do not regularly alternate, the longitudinal features, if present, are more closely spaced, cannot be traced over long distances, and occasionally occur as furrows as well as ridges on the same surface.

Also puzzling is the presence of a raised area at the centre of certain depressions marking leaf bases (text-fig. 2). Those illustrated in Plate 71, fig. 8 occur on a stem (type *b* preservation) adjacent to the holotype: removal of the stem distal to the leaf attachment sites has revealed the leaves themselves. The raised area on the left is elongate, that on the right more circular. The anatomical feature responsible for such a topography remains unknown.

Considering *Colpodexylon*, different appearances of the leaves may be related to the behaviour on compression of dorsoventrally flattened structures with extended horizontal connections with the stem. Seen sideways-on, such leaves appear as linear structures with slightly expanded bases (horizontal stem on Pl. 74, fig. 7) produced by the lateral compression of the unbranched proximal regions of the leaf. However, we encountered some such specimens in which removal of matrix immediately adjacent to the straight edge, believed to represent the abaxial limits of the leaf, revealed a further strip of more delicate coalified material below. This change in level and thickness suggests that the originally gently abaxially curved leaf had been twisted slightly on compression so that part of the dorsal (abaxial) surface has become visible at the lower level. A similar explanation fits the zoned appearance of certain quite broad leaf bases in which the adaxial quarter or one third is more heavily coalified or stained than the remainder below. Twisting or fracture of the extended flat or crescentic junction may account for the constrictions sometimes visible at leaf junctions (Pl. 74, fig. 9). As a result of twisting in the basal region of the leaf attached to the holotype (Pl. 74, fig. 2) the abaxial or adaxial surface is preserved in the same plane as the flattened stem.

PALAEOBIOGEOGRAPHY

Lack of information from southern continents has, more than any other factor, frustrated attempts to detect provincialism in Devonian floras (Edwards 1973; Edwards and Fanning 1985). The situation

in South America is typical, the plants (e.g. *Haplostigma* and *Palaeostigma*) are often poorly understood and independent dating of assemblages absent. Even for this relatively well-preserved assemblage from Venezuela the age determination is equivocal in that animal fossils are lacking in the beds containing the plants (Co₈ horizon in the Campo Chico Formation): an assemblage of brachiopods and pelecypods (Co₆ horizon) suggests a Givetian age (probably middle to late Givetian: Benedetto 1980, 1984) for the Co₆ horizon some 50 m below. Brachiopods and pelecypods from 300 m above the plant horizons are late Mississippian–early Pennsylvanian. Bowen (1972) mentions an assemblage of Middle to Upper Devonian palynomorphs (presumably Frasnian) from the upper part of the Campo Chico Formation but we have been unable to correlate this horizon with the plant beds. We have failed to isolate a spore assemblage from the matrix and spores found adpressed to several of the axes are not sufficiently well preserved to permit an age determination (Pl. 73, fig. 7). The plants described here support a Givetian–Frasnian age (Grierson and Banks 1963), although *C. trifurcatum* and *Haskinsia colophylla* are also recorded from Eifelian sediments in New York State. Of the assemblages from Argentina originally described by Frenguelli (1954) and reinvestigated by Menendez (1965*a, b*) only one, that containing *Haplostigma furquei*, is independently dated and considered Middle Devonian from associated trilobites. The far more diverse assemblage from the Quebrada de la Chavela including *Drepanophycus eximius* (Menendez 1965*b*) and *Archaeosigillaria conferta* (Menendez 1965*a*) as well as *Furqueia angladae*, *Charnelia dichotoma*, *Hyenia argentina*, and *Adiantites devonica* was originally thought to be Devonian but Cuerda *et al.* (1968) consider it younger (Carboniferous) after re-examination and re-identification of some of the plants.

Considering Brazil the assemblage from the Upper Porta Grossa Beds with a number of species of *Spongiophyton* and *Haplostigma* (Kräusel 1960) was originally described as Lower Devonian. Chaloner *et al.* (1974) reviewed recent palynological and micropalaeontological (acritarchs and chitinozoans) studies and concluded that the sediments are probably Givetian. Associated palynomorphs suggest that the lycopod assemblage (*Palaeostigma sewardi*, *Protolpidodendron kegei*, and *Archaeosigillaria picosensis*) in the Picos Formation of the Maranhao Basin (Kräusel and Dolaniti 1957) is Middle Devonian (Bär and Riegel 1974) although age determinations of other workers range from Emsian to Frasnian (Sampaio and Northfleet 1973; Brito 1967). Finally, strata on the Falkland Islands containing *H. irregularis* are considered Middle Devonian on the basis of the plants themselves (Seward and Walton 1923). These are being reinvestigated by Dr. Sergio Archangelsky.

Thus on current evidence, vascular plant assemblages from South America are of Middle Devonian age, and are dominated by lycopod genera, most of which are known from the northern hemisphere. The recent taxonomic and stratigraphic review of African lycopods (Anderson and Anderson (in press)) includes some revision of American lycopods, which reinforces similarities between the floras of the two southern continents. Further support for a uniform world-wide flora in mid-Devonian times comes from the description of *Leclercqia complexa* from Queensland (Fairon-Demaret 1974), and late Devonian sediments of New South Wales contain species of the northern hemisphere genera *Leptophloeum*, *Barinophyton*, and *Archaeopteris* (Gould 1975).

Our studies provide evidence for a uniform vegetation between a part of north Gondwana and the Old Red Continent (Laurentia) in mid- to late-Devonian times, but in isolation do not provide compelling evidence for global uniformity during that period. The similarities may simply reflect the palaeogeographic proximity of the localities or their occurrence in the same climatic zone encompassing more than one palaeocontinent. As far as is known the Venezuelan plants were homosporous with the potential for colonizing very wide areas (Chaloner and Sheerin 1979) and thus provide inconclusive evidence for the past distribution of continents. Many Devonian palaeogeographic reconstructions show an east–west (Rheic) ocean separating north and southern land masses (see e.g. Smith *et al.* (1981) where continent positions are based on palaeomagnetic data; Scotese *et al.* (1979); and Scotese (1984) late Devonian (B) map). Some recent reconstructions have closed or narrowed this ocean. That of Heckel and Witzke (1979), based on the distribution of palaeoclimatically significant rock types, e.g. carbonates, show northern parts of Africa and South America close to Laurentia (Old Red Continent), while Scotese (1984) presents an alternative

reconstruction for the late Devonian (map A) based on new palaeomagnetic data which positions Venezuela closer to north-east America, but Australia is at a much higher latitude and a considerable distance from the Old Red Continent. Such a juxtapositioning of Venezuela and eastern North America appears to complement our conclusions based on floras and receives further support from similarities in marine faunas comprising brachiopods, pelecypods, and corals (Benedetto 1980, 1984).

Finally, considering climatic zones, Barrett (in press) has predicted global climates for four reconstructions of continents in early- to mid-Devonian times including those of Smith *et al.* (1981) and Scotese *et al.* (1979). In all the models, he finds that northern South America (Amazon-Colombian) is likely to have been cool, the land vegetation growing under wet temperate conditions with eastern North America (Appalachian Basin) at lower latitudes in a tropical to subtropical wet climate. This suggests that these early pteridophytes with small or divided leaves and an abundance of strengthening tissues may have been tolerant of a range of climates and thus may provide an explanation for the apparent uniformity of vegetation in Devonian times. Alternatively it may merely indicate that such plants possessed a higher fossilization potential.

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